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RANGE AND VARIATIONS OF SUBSPECIES OF *CAMBARUS LONGULUS* (DECAPODA, ASTACIDAE)

By Hugo A. James [1]

As a result of the loss of the type specimens and confusion arising from an erroneous restriction of the type locality of the typical subspecies, the crayfish *Cambarus longulus* Girard, 1852, has been poorly understood; furthermore, the ranges of its two previously described subspecies have never been clearly delineated.

This report is based on a restudy of much of the material seen by previous authors and of representatives of all the collections of *C. longulus* in the U.S. National Museum (including those previously a part of the collection of H. H. Hobbs, Jr.). In addition, personal field studies within the ranges of all three subspecies herein recognized have supplemented the study of preserved specimens. A total of approximately 1300 specimens in 265 collections from 219 localities have been included.

The maps have been prepared from drainage, contour, and base maps obtained from the U.S. Geological Survey, Washington, D.C.

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[1] University of Bridgeport, Bridgeport, Connecticut.

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A History of the Species

1852. Girard, having examined specimens of crayfish of uncertain locality (somewhere "within the middle States of the Union"), concluded that they were sufficiently different from the then-known forms of *C. diogenes* and *C. bartonii* to warrant the designation *Cambarus longulus* (p. 90). In this work, he first employed *Cambarus* as a subgeneric name.

1870. The genus *Cambarus* was divided by Hagen into four groups (p. 31), *C. bartonii* being made the type for his Group III into which all similar forms were placed. Having examined Girard's type of *C. longulus,* Hagen indicated that it was probably an abnormal *C. bartonii* (pp. 78, 79) and he erroneously placed it in his Group III as "*Cambarus Bartonii.*"

1885. Faxon, having examined Hagen's description of Girard's type of *C. longulus,* as well as several similar specimens in the USNM collections, intimated that Girard's *C. longulus* was valid (1885a, p. 66), yet he did not consider his own total number of specimens sufficiently adequate to warrant reestablishing *longulus* as a species. Instead, on the basis of specimens taken from eastern Tennessee, West Virginia, and Cumberland Gap, Va., he described and named *longirostris* as a variety of the species *C. bartonii* (1885a, pp. 65, 66) and stated: "The specimens described above under the name of *C. bartonii* var. *longirostris,* perhaps are the same form as *C. longulus* . . . in accord with Hagen's description of Girard's type" (1885a, p. 66).

1890. Faxon ". . . after examining the large number of specimens (over one hundred, including females and both forms of the male) . . ." restored *longulus* "to the full rank of a species." The variety *longirostris,* however, was retained as a varietal form of *C. bartonii* on the basis of an inadequate number of specimens (pp. 623, 624). In this paper, Faxon erred in designating *C. longirostris* as *C. spinirostris* but corrected his own error: "(*lapsu calami pro 'longirostris'*)" (Faxon 1914, p. 424).

1898. In his "Observation on the Astacidae," Faxon listed several new localities for specimens of both "*Cambarus longulus* Girard" and "*Cambarus bartonii longirostris*" deposited in the USNM. It should be noted that he still retained the specific name of *longulus* (pp. 649–650).

1899. Hay, in "Synopsis of North American Invertebrates,"

placed *longirostris* with *C. longulus* as a subspecies of the latter (p. 966) and characterized both subspecies in a clear, concise key to the North American Astacidae.

1903. Harris, in a compilation of data (1903, p. 58), referred to *C. b. longulus* and *C. b. longirostris*. I have presumed this to be in error owing to Harris' interpretation of Faxon (1885a).

1905–1912. Having erected four subgenera of *Cambarus*, Ortmann established the subgenus *Bartonius* (1905, p. 120), which was declared a synonym of *Cambarus* for reason of priority by Fowler, who listed, in the place of *Bartonius*, the subgenus *Cambarus* (1912, pp. 340–341).

1914. For some unexplained reason, Faxon reduced *longulus* to subspecific rank calling it "*Cambarus bartonii longulus*" and retained *longirostris* as "*C. bartonii longirostris*." He completely omitted Hay's designation and wrote: "The character of the suborbital margin of the carapace seems to be very constant within the limits of a good subspecies, and it may prove to be the really diagnostic feature for separating *C. b. longulus* and *C. b. longirostris*" (pp. 389, 424). Fifteen years before, Hay (1899, p. 966) had utilized this identical diagnostic feature in his key.

1931. Ortmann, following Fowler, listed both "*Cambarus* (*Cambarus*) *longulus longulus* Girard (1852)" and "*Cambarus* (*Cambarus*) *longulus longirostris* (Faxon) (1855)" (pp. 118, 121). Ortmann considered the type locality for *longirostris* to be "The first *exact* locality given by Faxon ('85b) . . . Doe River, Carter Co., Tennessee" (p. 121).

1942. Ten years later, in a revision of the genus *Cambarus*, Hobbs, primarily adopting Ortmann's ideas of subgeneric relationships, elevated the previously recognized subgenera to the rank of genus within the new subfamily Cambarinae.

1959–1961. Hobbs (1959, p. 896) indicated that there are two subspecies of *Cambarus longulus* and subsequently indicated to the present writer that a third (form) probably should be recognized.

Cambarus longulus Girard

The species *Cambarus longulus* Girard (1852) belongs to the Bartoni Section (Ortmann, 1931, p. 105) of *Cambarus* Erichson (1846) (as redefined by Hobbs 1942a, p. 354) and, as herein recognized, consists of three subspecies: *Cambarus longulus longulus*, *C. longulus longirostris* Faxon, and *C. longulus chasmodactylus*, new subspecies.

Geographical limits—The limits of the range of the species *C. longulus*, although more specifically designated within the geographical discussions of the respective subspecies are: North: represented by *C. l. longulus*, in the upper James drainage in Greene County (on the eastern side of the Blue Ridge) and Highland County (to the

west of the Blue Ridge) in Virginia, and by *C. l. chasmodactylus* in Greenbrier drainage in Pocahontas County, W. Va. South: represented by *C. l. longulus* in the upper Yadkin drainage of Wilkes County (east of the Blue Ridge) and by *C. l. longirostris* in Will's Creek (Coosa River drainage), DeKalb County, Ala. East: in the upper piedmont province by *C. l. longulus* from the Rivanna River (James drainage), Fluvanna County, Va., southward to the Yadkin River in North Carolina. West: by *C. l. chasmodactylus* from the Greenbrier River in West Virginia and *C. l. longirostris* from a direct tributary to the Tennessee River in Lawrence County, Tenn. (Map 1).

Key to Subspecies of *Cambarus longulus*

1. Suborbital angle well defined and acute . . . . **longirostris** Faxon (1885)
   Suborbital angle markedly reduced or absent, never acute 2
2. Length of dactyl of chela less than twice the length of the inner margin of the palm . . . . . **longulus** Girard (1852)
   Length of dactyl of chela twice (or more) the length of the inner margin of the palm . . . . . **chasmodactylus**, new subspecies

Cambarus longulus longulus Girard

Cambarus longulus Girard, 1852, Proc. Acad. Nat. Sci. Philadelphia, vol. 6, p. 90.
Cambarus longulus Faxon, 1890 (part) pp. 623, 624.—Ortmann, 1902, p. 277.—Harris, 1903 (part) p. 107.—Fowler, 1912, p. 344.—Ortmann, 1913 (part), pp. 335, 337, 339, 352, 353, 375, 376.—Brimley, 1938, p. 503.
Cambarus Bartonii Hagen, 1870 (part), pp. 7, 9, 75, 78, 79.—Faxon, 1884 (part), p. 145; 1885a, pp. 11, 64, 66.
Cambarus bartonii longulus.—Faxon, 1885a, p. 66 (by implication).—Harris, 1903 (part), pp. 58, 107, 138, 142, 154–155, 159.—Faxon, 1914, pp. 390, 424.
Cambarus longulus longulus.—Hay, 1899 (by implication) (part), pp. 959, 966.—Ortmann, 1913 (part), pp. 336, 337, 375.—Hobbs 1950, p. 349; 1959 (part), 896.—Johnson, R. M., 1957, pp. 178, 182; 1959, pp. 181, 183.—Johnson, T. L., 1960, p. 229.
Cambarus (*Bartonius*) *longulus*.—Ortmann, 1905 (part), pp. 120, 122, 128, 129.
Cambarus (*Cambarus*) *longulus longulus*.—Ortmann, 1931 (part), pp. 106, 107, 108, 118–121, 123, 124, 128, 134.

Diagnosis.—Concolorous, or speckled, in shades of blue to orange. Rostrum with swollen margins, lacking marginal spines or tubercles, tapering somewhat abruptly to a short acumen, length .40–1.1 (average .95) times postorbital width. Suborbital angle and branchiostegal spines strongly reduced or absent; lateral spines or tubercles on carapace usually present, but absent in certain populations; postorbital spines and ridges weak. Areola from 29 to 42 (average 37) percent of length of carapace: 2.3–5.9 (average 3.5) times longer than broad; and with 4–6 punctations across narrowest part. Antennal scale 1.7–3.2 (average 2.5) times longer than broad (pl. 1*a*). Chela (pl. 1*j–m*) almost devoid of tubercles; inner margin of palm

with an indistinct row of weak serrations; all surfaces with scattered, deep punctations. Palm broad, with widely gaping (in adults), subcylindrical fingers which meet only at their tips; inner base of immovable finger with tuft of plumose setae in immature animals, and, except in upper James River, to some degree in older forms. Proximomesial angle of inner margin of palm strongly hooked proximally, forming, with carpus, a deep-curved acute angle (pl. 1*mm:* C); length of inner margin of palm (pl. 1*mm:* A) at least twice that of distance between spine of carpus and proximal extremity of inner margin of palm when the chela is fully extended (pl. 3*mm:* B) (in well over 75 percent of examined specimens). Width of palm .53–1.0 (average .80) times dactyl length; length of outer margin of chela 1.5–3.6 (average 2.7) times that of inner margin of palm and 1.0–2.6 (average 1.7) times greater than the length of dactyl. First pleopod of first-form male reaches coxa of third pereiopod when abdomen is flexed. (For detailed description of first pleopod of first-form male, see Hart, 1952, p. 47; Parish, 1948, figs. 2, 4.)

Remarks.—Faxon (1898, p. 650) (1914, pp. 389, 424) lists as *C. l. longulus* several collections which should be referred to *C. l. chasmodactylus* or *C. longulus longirostris;* Newcombe (1929, maps 268, 278, 286) and Fleming (1938) repeat the errors of Faxon. All collections erroneously recorded as *C. l. longulus* are listed by me with their proper designations in list I (p. 7).

Of the three subspecies, *C. l. longulus* appears to be the most variable. Although most populations possess a tuft of plumose setae at the base of the immovable finger of the chelae, those of the upper James drainage typically lack such a tuft. Ortmann (1931, pp. 118–124) notes the absence of lateral spines on the carapace of nine of his specimens of *C. l. longulus.* He was correct only with respect to a minority of populations; most have spines.

Some taxonomic characters, previously used by other investigators, must be disregarded or used only in part. Size, although of interest, gives little indication of subspecific variation; most *C. l. longulus* are, on the average, smaller than *C. longulus longirostris* or *C. l. chasmodactylus*; the carapace length of the largest first-form male *C. l. longulus* examined is 34 mm. and its hand length 29 mm. This male is larger than some first-form males of *C. longulus longirostris* and *C. l. chasmodactylus:* hence, size (sexually mature adults) as a taxonomic criterion must be used in combination with other characters. Color and color pattern of living specimens are sometimes useful in separating populations of *C. l. longulus* (speckled green to orange versus concolorous blue greens and browns). Color pattern is of slight intersubspecific value in that neither of the other

subspecies shows the speckled condition; however, neither do the majority of the population of *C. l. longulus*.

Specimens examined.—I have examined approximately 100 collections from 78 localities in Virginia, West Virginia, and North Carolina, including adults of both sexes, both forms of male, and juveniles, representing a minimum of 500 specimens. I have no authenticated records of this subspecies having been taken from Tennessee (see list III, p. 7).

Geographic distribution.—It would appear that *C. l. longulus* is limited geographically to the James, Roanoke, and Yadkin River systems of the Atlantic drainage (maps 1, 2). The southernmost record is from the Yadkin River drainage, Wilkes County, N. C. (map 2, no. 92). The northern limit seems to be in the headwaters of the James in Highland County, Va., west of the Blue Ridge (map 2, nos. 51–53) and in Greene County, east of it (map 2, nos. 43–50). It is found as far east as the Rivanna River (James drainage) and its tributaries (map 2, no. 36) but does not, from my data, extend west into or beyond the New River drainage or north into the Shenandoah as some records erroneously indicate (see lists I, II).

A list of all localities and drainage systems in which *C. l. longulus* has been found has been deposited with the U.S. National Museum.[2] Many collections incorrectly labeled as *C. l. longulus* must herewith be removed and reassigned to other taxa.

Because the labels for his type specimens had been lost, Girard (1852, p. 90) cites the locality only as "Middle States." Ortmann (1931, p. 118), listing the first of Faxon's reported localities (1890, p. 623), designates "the first exact locality . . . as a supplementary type-locality . . . South River, Waynesboro, Augusta Co., Virginia. (Faxon) (to Shenandoah and Potomac)." This choice of type locality seems inadmissible, for no member of the species *C. l. longulus* has been found since in the Potomac drainage. Neither Girard (loc. cit.) nor Hagen (1870, p. 78) mentions the presence of a lateral spine on the type specimen, but Hagen does note that between the fingers there "is a large bunch of hairs." From this combination of characteristics, it would seem more likely that Girard's type came from the James drainage, east of the Blue Ridge.

Synonymical reassignments.—On the basis of available data, many collections (listed below), previously recorded as *C. l. longulus*, now must be reassigned either to another species or to the subspecies *C. longulus longirostris* or *C. l. chasmodactylus*. Inappropriate names and/or localities are so indicated in the synonomy.

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[2] Copies may be obtained by writing to the author or to the U.S. National Museum, where these data are on file (no 254736) in the office of the Registrar.

List I

(Forms recorded as *C. l. longulus* that must be relegated to other species)

Faxon, 1890.	1. Waynesboro, Potomac River—no *C. longulus* are known from this drainage.
Harris, 1903.	2. A compilation of data, repeating the errors after Faxon 1884–1890.
Ortmann, 1913.	3. "Shenandoah River (Faxon)," Potomac drainage—see 1 above.
Ortmann, 1931.	4. As in Ortmann 1913—see 3 above.
Fleming, 1938.	5. Errors as in Faxon to 1914.

List II

(Forms recorded as C. *l. longulus* that must be relegated to C. *l. chasmodactylus*)

Faxon, 1890.	1. Wytheville, Va. (New River).
	2. Reed Creek, Wytheville, Va. (New River).
Hay, 1899.	3. Hay derived his key on the basis of known collections that include *C. l. chasmodactylus.*
Harris, 1903.	4. See list I, no. 2.
Ortmann, 1905.	5. Errors as in Faxon through 1898.
Ortmann, 1913.	6. Upper Kanawha River (presumed to be New River drainage; if not, this collection then belongs in list I).
	7. Greenbrier River (New River).
	8. New River.
Faxon, 1914.	9. Greenbrier River (New River).
	10. Bluestone River (New River).
Newcombe, 1929.	11. A compilation, errors as in Faxon, 1914 (list II, nos. 9, 10).
Ortmann, 1931.	12. A listing of known localities, errors as in Faxon, 1890 (list I, no. 1) and Ortmann, 1913 (list II, nos. 6, 7, 8).
Fleming, 1938.	13. Errors as in Faxon to 1914.
Hobbs, 1959.	14. According to collections on which Hobbs key was based, part of C. *l. longulus* belongs here.

List III

(Forms recorded as *C. l. longulus* that must be relegated to *C. longulus longirostris*)

Faxon, 1890.	1. South Fork of Holston River (Tennessee River)—*C. l. longulus* is entirely absent from Tennessee and the Tennessee River system.
	2. Spring Creek to French Broad River.
	3. Watauga River (Holston River).
	4. Knoxville, Tenn.
	5. Eastern Tennessee.
	6. Holston River drainage system.

Faxon, 1898.	7. Tennessee, Cumberland Gap.
	8. Tennessee, Tazewell.
	9. Tennessee, Greeneville.
	10. Tennessee, Knoxville.
Harris, 1903.	11. See list I, no. 2.
Ortmann, 1905.	12. Errors as in Faxon to 1898.
Ortmann, 1913.	13. Holston and Clinch River systems—corrected by Ortmann, 1931.
Brimley, 1938.	14. Lists both *C. l. longulus* and *C. longulus longirosilis*—both are *C. longulus longirostris* from French Broad drainage.
Fleming, 1938.	15. Errors as in Faxon to 1914.
Hobbs, 1959.	16. These forms of *C. l. longulus* from Tennessee and the Tennessee River system in southwestern Virginia are *C. longulus longirostris.*

List IV

(Other synonymical records not fitting into lists I, II, III)

Hagen, 1870	1. "A female type of *C. longulus* . . . differs from *C. Bartonii* in having its hands smooth . . . I think it is *C. Bartonii*"—This specimen more logically belongs to *C. l. longulus.*
Faxon, 1914	2. "I have seen an interesting lot of specimens (from above Kanawha Falls) that combine the characters of *C. b. montanus* and *C. b. longulus.* . . . These specimens are in the U.S. National Museum, No. 23990, and in the Museum of Comparative Zoology, No. 7401."—Having examined the former collection, the present writer, although uncertain of its specific status, excludes the above from the *C. longulus* group.

Coloration and color pattern.—Most *C. l. longulus* are concolorous, usually a brown or green with shades of ivory to tan beneath. A mottled pattern is known from two widely separated localities (fig. 2*c*). One, the Swift Run, a tributary of the North Fork of the Rivanna River (James drainage) in Greene County, Va. (map 2, no. 50) is entirely of the brown phase (orange to dark brown). The other mottled pattern is found in some tributaries of the Smith and South Mayo Rivers (Dan River to Roanoke drainage) in Patrick County (map 2, nos. 65–70); these are variously colored within individual populations. Colors range from yellow orange through shades of green and brown and, like the James River specimens, have their underparts tinted ivory to tan. It would appear that the background color of these mottled "Roanoke *longulus*" is in shades of tan and that only the mottling seems to vary. These two very similarly patterned and colored populations of crayfish occur in streams almost 125 miles apart.

***Cambarus longulus longirostris* Faxon**

Cambarus Bartonii var. *longirostris*.—Faxon, 1885a, Mem. Mus. Comp. Zool., vol. 3, p. 64; 1885a (part), p. 64; 1885b, p. 358; (as *C. bartonii longirostris*); 1890, pp. 623, 624; 1898 (part), p. 649.—Harris, 1903 (part), pp. 58, 75, 154.—Ortmann, 1905 (part), pp. 128, 129, 135.—Faxon, 1914, pp. 389, 424.—Newcombe, 1929, p. 286.

Cambarus bartonii spinirostris.—Faxon, 1890, pp. 623, 624.

Cambarus longulus.—Faxon, 1890 (part), pp. 623, 624; 1898 (part), p. 650.—Harris, 1903 (part), pp. 58, 107, 138, 154, 155, 159.—Ortmann, 1913 (part), pp. 335, 337, 362, 375.—Fleming, 1938, pp. 299, 300, 301.—Brimley, 1938, p. 502.—Hobbs, 1959 (part), p. 898;

Cambarus longulus longirostris.—Hay, 1899, pp. 959, 966; Johnson, 1957, pp. 178, 182; 1959, pp. 181, 183.—Hobbs, 1959 (part), p. 898.

Cambarus (*Cambarus*) *longulus longirostris*.—Ortmann, 1931 (part), pp. 121–124.

Cambarus longerosilis Brimley, 1938, p. 503.

DIAGNOSIS.—Concolorous in shades of blue green through orange, or bicolorous with two dark dorsal saddles of varying widths; one on posterior part of carapace and the other immediately cephalic to cervical groove (figs. 2*a,b*). Rostrum with strongly swollen margins, without spines or tubercles, abruptly tapering to moderately short acumen, length .78–1.1 (average 1.0) times postorbital width. Suborbital angle and postorbital spines and ridges strong (pl. 1*r*). Branchiostegal spines and lateral spines or tubercles on carapace absent. Length of areola 2.3–5.9 (average 4.0) times width, 30–39 (average 36) percent of length of a carapace, and with 3–10 punctations across narrowest part (average 7–8). Antennal scale 1.7–3.0 (average 2.3) times longer than broad. Chela mostly as in *C. l. longulus* (pl. 1*n,o*), length of outer margin of chela 1.5–1.8 (average 1.7) times length of dactyl and 2.6–4.4 (average 3.1) times length of inner margin of palm, length of dactyl of chela 1.5–3.0 (average 1.9) times length of inner margin of palm, and width of palm .52–.88 (average .72) times length of dactyl. First pleopod of first-form male as pictured (pl. 1*f,g*).

REMARKS.—Faxon (1885a, p. 64) indicates that his collection of three specimens"from Cumberland Gap (Claiborne Co., Tenn.) have well-marked lateral spines on the carapace." Since the chela of this Powell River form differs from that of the typical *C. longulus*, it is, presumably (awaiting further data), other than the species *C. longulus*. Some specimens of *C. longulus longirostris* do have a minute tubercle in place of the lateral spine.

Little difference exists between *C. longulus longirostris* and the other two subspecies. Variations in all characteristics thus far observed, exclusive of the suborbital angle, overlap to some degree those of the other subspecies: average ratios calculated for *C. longulus longirostris* usually lie midway between those calculated for *C. l.*

longulus and *C. l. chasmodactylus*. The setaceous tuft at the base of the immovable finger of the chela may be present or absent but, as in *C. l. longulus*, it seems to be consistent within a population; older, late intermolt animals do not seem to lose the tuft of setae as readily as do those of *C. l. longulus* or *C. l. chasmodactylus*. Most *C. longulus longirostris* are larger than *C. l. longulus* and smaller than *C. l. chasmodactylus*. The largest, a first-form male, has a carapace that measures 43 mm. in length and a chela, 56 mm. long. Both color and color pattern vary in different parts of the range; figures 2*a,b* illustrate two of the pattern variations. Neither *C. l. longulus* nor *C. l. chasmodactylus* possesses the vivid saddle pattern seen in so many *C. longulus longirostris* populations, particularly those orange-colored animals from Lawrence County and the less colorful individuals from the Hiwassee drainage, Tennessee. Most *C. longulus longirostris* are a blue green or brown not unlike the concolorous *C. l. longulus*.

There are so many variations in this crayfish that, beyond the presence of the suborbital angle, no characteristic has been observed that will serve to distinguish *C. longulus longirostris* from the other subspecies.

Specimens examined.—I have examined approximately 500 specimens from 113 collections taken from 97 localities in Alabama, Georgia, North Carolina, Tennessee, and Virginia. Many of these collections contain both sexes and both forms of the male.

Geographic distribution.—*Cambarus longulus longirostris* is confined to tributaries of the Tennessee and Coosa Rivers. Reports from the Clinch River, "West Virginia" are erroneous; the Clinch River, Tennessee drainage, does not extend into West Virginia; one need only note this location to know that Faxon erred and probably meant Clinch River in western Virginia. The northern limit appears to be in the upper Clinch (map 2, no. 202), Tazewell County, Va.; its southernmost boundary is Will's Creek (Coosa drainage) (map 1, no. 96), DeKalb County, Ala. Having recorded five collections from Will's Creek in DeKalb County, I believe it is highly probable that this is the locality meant by Faxon (1898, p. 649), not "Will's Creek, *Pollard, Escambia Co.* [italics mine], Alabama." I have no knowledge of a Will's Creek in Escambia County. Ortmann (1931, p. 123), assuming that the county listed by Faxon was correct, notes this record as being "extremely doubtful" giving instead as the southernmost locality, Catoosa County, Ga. (Tennessee River drainage). Two collections from Lawrence County, (map 1, nos. 209, 210) and one from Lauderdale County, Ala. (map 1, no. 98) mark the westernmost limit of the range. Although many collections have been made both east and west of the southwestern localities, no *C. longulus longirostris* has been found closer than those collected from Marion

County, Tenn. (map. 1, nos. 143–145). It would seem that here the ecologically restricted *C. longulus longirostris* has been forced into its isolated strongholds by the invasion of members of the genus *Orconectes*. It is probable that these western records, especially those of Lawrence County, Tenn., are relict populations. No ecological data are available for the Lauderdale, Ala. specimens, although I suspect they would conform to those of Lawrence County. The northeastern limit is marked by the North Fork of the Holston River, Bland County, Va. (map. 2, no. 186).

That the three subspecies of *C. longulus* are allopatric is clearly evidenced where the headwaters of separate drainage systems interdigitate. For example, White Top Creek (map 2, near no. 195) northeast of Konnarock, in Smyth County, Va. (Holston drainage), in which *C. longulus longirostris* is found, is less than a mile from Lewis Creek (map 2, no. 248) near Troutdale, Grayson County (new drainage) where *C. l. chasmodactylus* occurs.

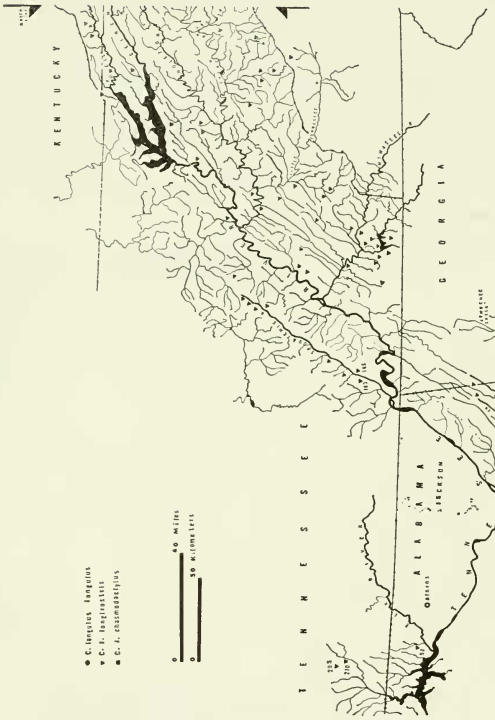
In many localities *C. longulus longirostris* is particularly abundant; in one such locality (map 2, no. 195), Big Laurel Creek, Smyth County, Va., Hobbs (personal communication) collected 99 specimens in a single seine haul over approximately 100 square feet.

Ortmann (1931, p. 123) wrote that *C. longulus longirostris* had "not been found in the Tennessee River below Knoxville, and the mouth of the Clinch, nor in its eastern tributaries (Little River, Little Tennessee, and Hiawassee [sic] Rivers)." I have recorded specimens from Louden County (below Knoxville), Roane County (below the mouth of the Clinch); Monroe County (Little Tennessee), McMinn, Bradley, and Polk Counties (Hiwassee); also previously unrecorded are localities in Lawrence County, Tenn., Lauderdale County, Ala., and Armuchee Creek, Floyd County, Ga. (Coosa drainage).

Faxon's type locality (1885b, p. 358) is "Doe River, Elizabethon, Carter County, Tenn.," from which he had three females. Ortmann (1931, p. 121), Hobbs, and Holt subsequently have collected specimens from this locality (map 2, no. 112).

The only incorrect listing of *C. longulus longirostris* of which I am aware is "Cumberland Gap" (Faxon, 1885a), as previously discussed. This locality has been repeated in Faxon (1898), Harris (1903), and again in Ortmann (1931). The error is logical; except for the difference in chelae and the presence of lateral spines on the carapace, this form is superficially much like *C. longulus longirostris*.

Those locality records listed by previous authors for *C. l. longulus* that actually apply to *C. longulus longirostris* are included in list III, p. 7.



Map 1.—Distribution and range of *Cambarus longulus* (numbers refer to collection localities).

MAP 2.—Distribution and range of *Cambarus longulus* (numbers refer to collection localities).

***Cambarus longulus chasmodactylus*, new subspecies**

Cambarus Bartonii Hagen, 1870 (part), p. 76.—Faxon, 1885a (part), pp. 60, 61.
Cambarus longulus Faxon, 1890 (part), pp. 623, 624.—Ortmann, 1913 (part), pp. 335, 337, 375.
Cambarus longulus longulus.—Hay, 1899 (part), pp. 959, 966.—Hobbs, 1959 (part), p. 898.
Cambarus bartonii longulus.—Harris, 1903 (part), pp. 58, 107, 138, 146, 148, 154, 155, 159.—Faxon, 1914, p. 389, 390.—Newcombe, 1929, map, pp. 268, 278, 280, 286.
Cambarus (*Bartonius*) *longulus*.—Ortmann, 1905 (part implied), pp. 120, 122, 128, 129.
Cambarus (*Cambarus*) *longulus longulus*.—Ortmann, 1931 (part), pp. 106, 107, 108, 118–121, 123, 128, 134–136.
Cambarus subspecies.—Johnson, 1957, pp. 178, 182; 1959, pp. 181, 183.

Diagnosis.—Concolorous, blue green tinged with shades of cream to rust. Rostrum with strongly swollen margins, without marginal spines or tubercles, acumen tapering abruptly to upturned apex, with a punctate depression posteromedially; length of rostrum 1.5–2.2 (average 1.9) times longer than wide; .69–1.1 (average 1.0) times postorbital width and .17–.28 (average .23) times carapace length. Suborbital angle and branchiostegal spines absent, lateral spines absent except in specimens from one locality in Carroll County, Va. (map 2, no. 240); postorbital ridges and spines strong, cheeks with scattered low tubercles. Areola 3.5–6.0 (average 4.4) times longer than broad, length 34–37 (average 27) percent of length of carapace and with 4–10 (average 6–7) punctations across narrowest part. Antennal scale 1.6–2.7 (average 2.2 times longer than broad), spine strong. Inner margin of palm of chela with a row of squamous tubercles, remainder smooth; all surfaces with scattered, deep punctations, some on dorsal surfaces form linear rows. Palm broad, fingers of adults intensely gaping, meeting only at tips; immovable finger, subtriangular in cross section, with basal tuft of plumose setae, frequently reduced or absent in adult forms (pl. 1*y,z*) but present in all juveniles (pl. 1*w,x*); dactyl ovate to subcylindrical in cross section. Both fingers with single row of low tubercles on opposable surfaces, single tubercle near distal end of immovable finger often enlarged. "Hook" of proximomesial angle in inner margin of palm weak or obsolete, forming with carpus a deep weakly curved obtuse angle (pl. 1*zz:* C); length of inner margin of palm (pl. 1*zz:* A) of fully extended chela less than twice that of distance between spine of carpus and proximal extremity of inner margin of palm (pl. 1*zz:* B). Width of palm .48–.74 (average .61) times length of dactyl, length of outer margin of chela 2.6–4.7 (average 3.6) times length of inner margin of palm and 1.2–1.8 (average 1.6) times greater than length of dactyl. First pleopod of first- and second-form males and annulus ventralis of fe-

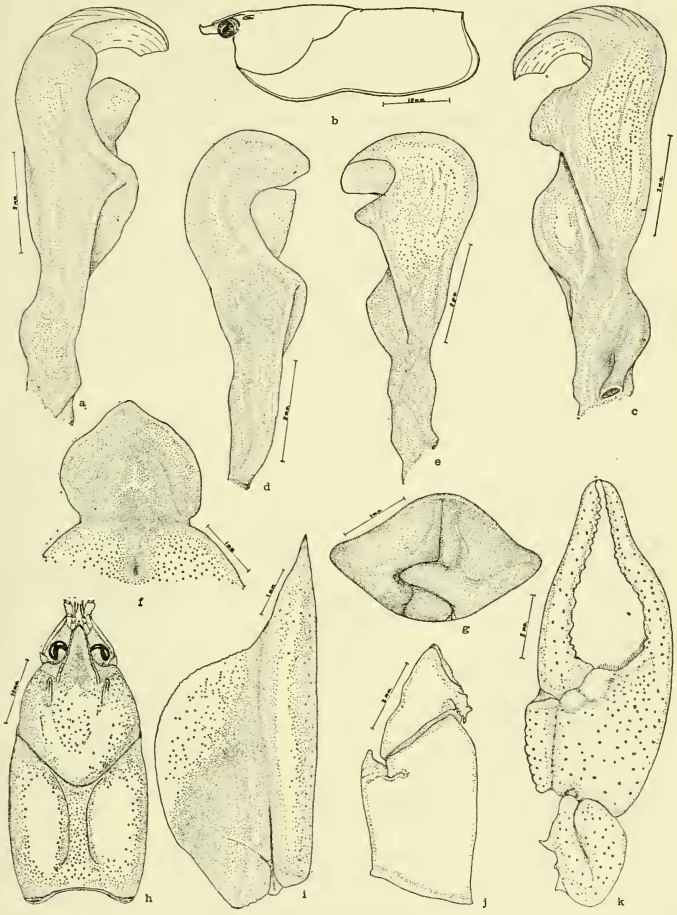


FIGURE 1.—*Cambarus longulus chasmodactylus*, new subspecies: *a*, lateral view of first pleopod of first-form male; *b*, lateral view of carapace; *c*, mesial view of first pleopod of first-form male; *d*, lateral view of first pleopod of second-form male; *e*, mesial view of first pleopod of second-form male; *f*, epistoma; *g*, ventral view of annulus ventralis; *h*, dorsal view of carapace; *i*, upper surface of right antennal scale; *j*, basipodite and ischiopodite of third right pereiopod of first-form male; *k*, upper surface of right chela and carpus of first-form male.

male imperceptibility different from *C. l. longulus* (pl. 1*d,e,u;* figs. 1*a,c–e,g*).

HOLOTYPE MALE, FORM I.—Body about 1.5 times broader than deep. Greatest width of carapace at level of midlength of areola (21.4 mm.). Abdomen shorter than carapace (34.0 and 39.7mm.) and narrower (16.0 and 21.4). Areola about 4.1 times longer than broad with six punctations across narrowest part. Cephalic section of carapace about 1.6 times length of areola. Areola about 38 percent of entire length of carapace (figs. 1*b,h*).

Rostrum with thickened margins, without marginal spines or tubercles, gently tapering, dorsally concave with deep punctations scattered in caudally situated oval depression; rostrum with thickened, cephalically converging margins forming an indistinct acumen with upturned apex, a row of setaceous punctations along mesial base of thickened margins. Subrostral ridges weak but visible along entire length of rostrum in dorsal aspect.

Postorbital ridges conspicuous, terminating cephalically in a small corneous spine; grooves of postorbital ridges well developed and bearing fine setae. Suborbital angle obsolete, replaced by a slight rounded projection just above level of base of antenna. Branchiostegal spine reduced to a small angular prominence. Carapace without lateral spines. Upper surface of carapace and lateral portion of branchiostegites punctate. Few granulations on lateral surface immediately caudal to cervical groove, but many on cephalolateral regions.

Cephalic section of telson with two spines in each caudolateral corner. Epistome with a slight cephalomedian projection (fig. 1*f*).

Antennules of usual form with a strong spine present on ventral side of basal segment. Antennal scale broadest just proximal of midlength, with outer distal margin terminating in a long, acute, corneous spine.

Right chela (fig. 1*k*) conspicuously punctate above and below, flattened, and about twice wider than deep (20–10 mm.). Inner margin of palm with single median row of nine squamous tubercles scarcely rising above contour of margin; longitudinal row of deep punctations present above and lateral to row of squamous tubercles. Upper surface of palm with two large tubercular swellings at base of dactyl. Immovable finger strongly convex laterally and without well-defined grooves or ridges; proximal half subtriangular in cross section, distal half ovate; basal portion almost as deep as wide; opposable margin with a tuft of setae proximally and with a more distal row of 16 rounded, corneous tubercles; larger tubercle present just below tubercular row and slightly distal to midlength; a row of minute denticles on distal third of opposable margin just ventral to

row of tubercles. Dactyl convex mesially along proximal two-thirds and without ridges or grooves. Concave opposable margin with row of 18 rounded corneous tubercles and distal third with a row of minute denticles ventral to tubercular row.

Carpus of right pereiopod longer than broad (14.0–10.5 mm.), with a deep longitudinal furrow above. Dorsal and lateral surfaces punctate; mesial surface with one large spinous tubercle near mid-length and a much smaller one proximally; ventral surface with two tubercles on distal margin.

Merus of first right pereiopod punctate laterally and mesially. A small tubercle near upper distal margin. Lower surface with a row of eight tubercles mesially (the two most distal enlarged and spinous), and two laterally.

Hooks on ischiopodites of third pereiopods only (fig. 1*j*); hooks heavy and projecting proximally a little beyond distal end of basipodite. Coxae of fourth pereiopods with caudomesial swollen prominences.

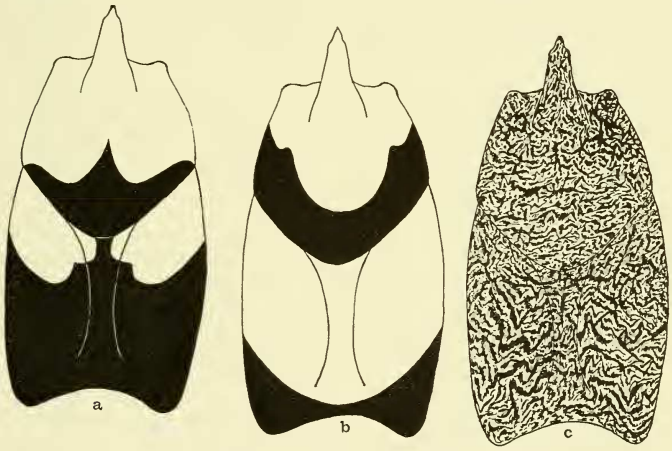


FIGURE 2.—*a*, Saddle pattern of "orange phase" of *Cambarus longulus longirostris* from Lawrence County, Tenn.; *b*, saddle pattern of the less colorful phase of *C. longulus longirostris* from Hiwassee drainage system in Polk County, Tenn.; *c*, a mottled phase of *C. l. longulus* from Dan River headwater (map 2, no. 70).

First pleopod reaching coxopodite of third pereiopod when abdomen is flexed. Tip terminating in two parts (figs. 2*a*, *c*); mesial process bulbous, noncorneous, bent caudolaterally and bearing a minute spine at its tip. Slight shoulder on lateral surface arising gradually from base of central projection.

Morphotype male, form II.—Differs from the holotype as follows: Cephalic section of telson with three spines in right and two in left caudolateral corners. Minute spinelike tubercle on left side of carapace immediately caudal to cervical groove. Areola with seven punctations across narrowest part. Inner margin of palm of chela, with a row of six squamous tubercles; opposable margin of immovable finger with 17 tubercles and that of dactyl with 19. Upper distal portion of merus with two tubercles and lower surface with a mesial row of ten tubercles. Hooks on ischiopodite of third pereiopods much reduced in size. First pleopod without corneous elements (figs. 1*d*, *e*); swollen prominence of fourth pereiopods smaller.

Allotype female.—Differs from the holotype as follows: Areola with five punctations across narrowest part. Opposable margin of immovable finger of right chela with 13 rounded tubercles, and that of dactyl with 15. Upper distal portion of left merus with two tubercles and lower surface with mesial row of seven. Rhomboid annulus ventralis with a high V-shaped ridge caudally and a medial longitudinal trough, deepest at apex of bend in sinus; sinus originates at caudal end of trough, makes a V-shaped arc dextrally and then bends caudally cutting midcaudal margin of annulus (pl. 1*u*; fig. 1*g*).

Measurements (in millimeters) of *C. l. chasmodactylus* are as follows:

	holotype	*allotype*	*morphotype*
rostrum			
length	9.1	8.4	8.3
width	4.5	4.3	4.2
postorbital ridges (distance between)	9.1	8.5	8.9
carapace			
maximum depth	14.3	14.0	15.0
maximum width	21.4	20.0	21.6
length	39.7	36.5	38.8
cephalic length	24.2	22.0	24.0
areola			
length	15.2	14.1	14.9
width	3.7	2.6	3.4
abdomen			
length (including telson)	34.0	34.5	35.0
width (at widest part)	16.0	17.7	16.6
antennal scale			
length	5.1	5.1	5.6
width	2.5	2.5	2.6
right chela			
palm width	20.0	14.0	17.5
palm depth	10.0	7.5	8.8
inner margin of palm length	13.6	9.1	11.7
right chela hand (outer margin)			
length	47.2	32.0	42.9
length of dactyl	29.0	20.6	27.8
right carpus			
length	14.0	9.0	12.0
width	10.5	8.0	9.0

Ratios of measured characters of *C. l. chasmodactylus* are as follows:

	holotype]	*allotype*	*morphotype*
carapace W/L	1.50	1.40	1.44
L of cephalic part of carapace; areola L	1.59	1.56	1.61
Rostrum L/carapace L	.23	.23	.21
Rostrum L/W	.20	.20	.20
Rostrum L/postorbital width	1.00	.99	.94
areola L/W	4.10	5.40	4.40
areola L/carapace L	.38	.39	.38
antennal scale L/W	2.40	2.00	2.20
palm of chela W/L of dactyl	.69	.68	.63
hand of chela L/L inner margin of palm	3.50	3.50	3.70
hand of chela L/L of dactyl	1.60	1.60	1.50
dactyl of chela L/L inner margin palm	2.10	2.30	2.40

TYPE-LOCALITY.—"East Fork of the Greenbrier River 9.7 mi. W. of Virginia State line on U.S. Hwy. 250, Pocahontas County, West Virginia [map 2, no. 263]. Here the river is between 50 and 100 feet in width and up to 3 feet in depth. Its slightly clouded water flows sluggishly to moderately over tilted bed rock strata on which are strewn many stones and a considerable amount of silt. The crayfish are abundant and lie concealed beneath the loose rocks" (Hobbs, pers. comm.).

DISPOSITION OF TYPE.—The holotype male (USNM 115513), allotype female (USNM 115514), and the morphotype male (USNM 115516) are deposited in the U.S. National Museum. Of the remaining 161 paratypes (USNM 115515), 17 males, Form I, 5 males, Form II, 16 females, 3 juvenile males, and 2 juvenile females are also in the U.S. National Museum; 7 males, Form I, 5 males, Form II, and 1 female are in: (a) Museum of Comparative Zoology, Harvard; (b) the collection of G. H. Penn, Tulane University; (c) the collection of Alejandro Villalobos, Institute de Biologia, Mexico, D.F.; and (d) 2 males, Form I, 2 males, Form II, 2 females, and 1 juvenile male are in the collection of the author at the University of Bridgeport, Bridgeport, Conn.

REMARKS.—Ortmann (1931, p. 120) was aware of the differences between *C. l. longulus* and *C. l. chasmodactylus* and wrote that in those "specimens from the New River drainage . . . the moveable finger may be over twice as long as the inner margin of the palm." This has been a completely reliable characteristic for distinguishing all the normal (chelae unregenerated) specimens I have seen.

On the basis of Faxon's work (1885a, pp. 60, 61; 1890, p. 623), I suspect that Hagen's "Greenbrier River" record (1870, p. 76) is *C. l. chasmodactylus*, but I do not have sufficient information to synonymize it. Further investigation may identify the above as well as Faxon's records of "Reed Creek, West of Wytheville, Wythe Co.,

(Virginia)"; and those "near White Sulphur Springs, Greenbrier Co., West Va." (1885a, pp. 60, 61) as *C. l. chasmodactylus*.

While *C. l. longulus* is the most variable of the subspecies, *C. l. chasmodactylus* appears to be the most stable. Little or no differences occur between even widely separated populations. One exception is the collection of nine specimens from Carroll County, Va., in which all juveniles and adults (as well as males and females) possess strong lateral spines on the carapace. This collection (map 2, no. 240) was made in a tributary of Crooked Creek (New River drainage). All other specimens including those from Reed Island Creek, an adjacent tributary to the New River, lack these lateral spines. Additional collecting in this area will be necessary before further comment may be made.

The largest available specimen of *C. l. chasmodactylus* is a female with a carapace length of 55 mm.; the largest chela I have seen measures 78 mm. in length by 26.5 mm. in width; only the hand of this animal is available. Size, however, must be disregarded as a diagnostic feature since many first-form males have a carapace length as little as 30 mm. and, as noted, the largest first-form male of *C. l. longulus* (the smallest of the subspecies) is 34 mm.

Specimens examined.—I have examined approximately 275 specimens in 56 collections from 44 localities; all are confined to the New River drainage system of North Carolina, Virginia, and West Virginia.

Entirely confined to the New River system, the known range of *C. l. chasmodactylus* extends northward to the upper reaches of the Greenbrier River in West Virginia (map 2, nos. 261–268); the most southern record is from Watauga County, N.C., in the headwaters of the South Fork of the New River (map 2, no. 229). Both eastern and western boundaries are formed by those Appalachian Mountains delimiting the New Valley.

There appears to be complete geographic isolation between this and the other two subspecies. In Alleghany County, N.C. (map 2, no. 215), *C. l. chasmodactylus* was collected from a tributary of the New River only a few miles from where *C. l. longulus* was collected in the Yadkin drainage in Wilkes County (map 2, no. 105), but nowhere in the entire range is there evidence of sympatry.

Ecological Distribution

The general habitat of the species *Cambarus longulus* has been noted by various investigators (Ortmann, 1913, pp. 375, 376; 1931, pp. 119, 123; Hobbs, 1950, p. 349; Reid, 1961, p. 249). Members of *C. longulus* are highly restricted stream or river inhabitants that live under or between rocks, away from the shore, in moderate to swiftly flowing, cool to cold water. The species does not, from all

accounts, frequent quiet pools, springs, or mountain "feeder brooks." Stream beds are typically of rock-strewn sand or gravel and relatively free of silt deposits.

Most specimens of *C. l. longulus* were taken from riffle areas in the lower mountain or upper piedmont streams. The water, clear or comparatively so, ranges from 2°–24° C. The current, over riffles, has been recorded as moderate to rapid. In streams with both pool and riffle areas, *C. l. longulus* was found only in the riffles. Stream beds of sand or gravel and strewn with rocks are characteristic of the habitats in which this crayfish usually is found. The size of the stream seems to have little, if any, influence on whether or not *C. l. longulus* frequents it.

The subspecies *C. l. chasmodactylus* varies from the typical subspecies in seeming to prefer larger, often turbulent streams. It is found abundantly in Reed Creek, Wythe County, Va.; typically, this animal, as described by Ortmann (1931, p. 119) lives "in the usual way under stones in *flowing water* [italics mine]."

Of the three subspecies, *C. longulus longirostris* is by far the least ecologically restricted. A cursory examination of the wide distribution (maps 1, 2) should suggest the apparent adaptability of this crayfish to the larger streams and rivers as well as to the smaller tributaries. In McMinn County, Tenn., it was found to be numerous in beds of *Nasturtium* sp. in a spring run; nearby, occasional animals were found in debris littering a stream bed of silt and sand, where there were but few rocks.

Serological Affinities

Johnson, in 1957 and again in 1959, using agar diffusion and tube precipitation techniques, serologically compared, among others, the three subspecies of *Cambarus longulus* (*Cambarus* sp. = *C. l. chasmodactylus*). Antigen (crayfish serum) and antibody (rabbit anti-crayfish serum) reactions, when compared (1957, p. 182; 1959, p. 183), indicate the close affinities of the three.

Summaries of Ratios

The tabulation below summarizes the collective quantitative data (figures of each column represent ratios of measurements of selected characters; upper row, minimum ratio; middle, maximum; lower, average):

Characteristic Ratio	*longulus*	*longirostris*	*chasmodactylus*
	0. 10	0. 19	0. 17
rostrum L/carapace L	0. 26	0. 28	0. 28
	0. 20	0. 22	0. 25
	1. 1	1. 3	1. 5

Characteristic Ratio	*longulous*	*longirostris*	*chasmodactylus*
rostrum L/W	2. 2	2. 3	2. 2
	1. 6	1. 8	1. 9
	0. 40	0. 78	0. 69
rostrum L/post orbital W*	1. 1	1. 1	1. 1
	0. 95	1. 0	1. 0
	2. 3	2. 3	3. 5
areola L/W	5. 9	5. 9	6. 0
	3. 5	4. 0	4. 4
	0. 20	0. 30	0. 34
areola L/carapace L	0. 42	0. 39	0. 47
	0. 37	0. 36	0. 37
	1. 7	1. 7	1. 6
antennal scale L/W	3. 2	3. 0	2. 7
	2. 5	3. 3	2. 2
	0. 53	0. 52	0. 48
palm W/dactyl L	1. 0	0. 88	0. 74
	0. 80	0. 72	0. 61
	1. 5	2. 6	2. 6
hand of chela L/inner palm margin L	3. 6	4. 4	4. 7
	2. 7	3. 1	3. 6
	1. 0	1. 5	1. 2
hand of chela L/dactyl L	2. 6	1. 8	1. 8
	1. 7	1. 7	1. 6
	1. 3	1. 5	2. 0
dactyl of chela L/inner palm margin L	2. 0	3. 0	3. 4
	1. 6	1. 9	2. 4

*Distance between anterolateral margins of postorbital spines or ridges.

Summary

As a result of the present study, three allopatric subspecies of *Cambarus longulus* Girard have been recognized. *Cambarus longulus longulus* is found in the lower mountain and piedmont streams of the Atlantic drainage, from the James south to the Yadkin Rivers. *Cambarus longulus chasmodactylus*, herein described, is restricted to the New River system from North Carolina to western West Virginia. *Cambarus longulus longirostris* frequents the Tennessee drainage system above Wilson reservoir, and the Coosa River drainage in northwestern Georgia and eastern Alabama.

Although all three subspecies are associated with riffle areas of lotic habitats, *C. longulus longirostris* appears to have a broader ecological tolerance than do the two other subspecies.

While *C. l. chasmodactylus* exhibits few variations throughout its range, *C. l. longulus*, perhaps because of its low vagility, has within its range several recognizable local populations.

It is concluded that these three crayfishes represent offshoots of a common stock which, while believed to be not too far removed from the primitive members of the genus, have become, for the most part, ecologically, highly specialized for life in restricted areas of "young" but not "infant" streams.

Literature Cited

Brimley, C. S.

1938. The insects of North Carolina, 560 pp.

Erichson, W. F.

1846. Übersicht der Arten der Gattung Astacus. Arch. für Naturg. vol. 12, no. 1, pp. 86–103.

Faxon, Walter

1884. Descriptions of new species of *Cambarus:* To which is added a synonymical list of the known species of *Cambarus* and *Astacus*. Proc. Amer. Acad. Arts Sci., vol. 20, pp. 107–156.

1885a. A revision of the Astacidae. Mem. Mus. Comp. Zool., vol. 10, no. 4, pp. 1–186, 10 pls.

1885b. A list of the Astacidae in the United States National Museum. Proc. U.S. Nat. Mus., vol. 8, no. 23, pp. 356–361.

1890. Notes on North American crayfishes, family Astacidae. Proc. U.S. Nat. Mus., vol. 12, no. 785, pp. 619–634.

1898. Observation on the Astacidae in the United States National Museum and in the Museum of Comparative Zoology, with descriptions of new species. Proc. U.S. Nat. Mus., vol. 20, no. 1136, pp. 643–694, pls. 62–70.

1914. Notes on the crayfishes in the United States National Museum and in the Museum of Comparative Zoology, with descriptions of new species and subspecies to which is appended a catalogue of the known species and subspecies. Mem. Mus. Comp. Zool., vol. 40, no. 8, pp. 347–427, pls. 1–11.

Fleming, R. S.

1938–1939. The larger Crustacea of the Nashville region. Journ. Tennessee Acad. Sci., vol. 13, no. 4, p. 296–324; vol. 14, no. 2, p. 261–264; vol. 14, no. 3, pp. 299–324.

Fowler, H. W.

1912. Crustacea of New Jersey. Rep. New Jersey State Mus., 1911, pt. 2, p. 31–650, pls. 1–150.

Girard, C.

1852. A revision of the North American Astaci, with observations on their habits and geographical distribution. Proc. Acad. Nat. Sci. Philadelphia, vol. 6, pp. 87–91.

Hagen, H. A.

1870. Monograph of the North American Astacidae, 3. Cat. Mus. Comp. Zool., no. 3, pp. 1–109, pls. 1–11.

Harris, J. A.

1903. An ecological catalogue of the crayfishes belonging to the genus *Cambarus*. Kansas Univ. Sci. Bull., vol. 2, no. 3, pp. 51–187.

Hart, C. W.

1952. The exoskeleton and musculature of the appendages of the first three abdominal segments of *C. longulus longulus* Girard (Decapoda, Astacidae). Virginia Journ. Sci., vol. 3, pp. 39–48.

Hay, W. P.

1899. Synopses of North American invertebrates, 6: The Astacidae of North America. Amer. Nat., vol. 33, pp. 957–966.

Hobbs, H. H., Jr.
1942. A generic revision of the crayfishes of the subfamily Cambarinae (Decapoda, Astacidae) with the description of a new genus and species. Amer. Mid. Nat., vol. 28, no. 2, pp. 334–357.
1950. Observations on the ecological distribution of three Virginia crayfishes. Virginia Journ. Sci., vol. 1, n. s., no. 4, p. 349.
1959. *In* W. T. Edmondson, Fresh water biology, xix+1248 pp., figs. 3.1–46.1.

Johnson, R. M.
1957. The Agar diffusion technique as applied to the study of serological relationships among crayfishes. Virginia Journ. Sci., vol. 3, pp. 177–184.
1959. Serology of crayfishes. Virginia Journ. Sci., vol. 10, n. s., no. 3, pp. 181–185.

Johnson, T. L.
1960. Histological observations on the sperm duct of *Cambarus longulus* Girard. Trans. Amer. Micros. Soc., vol. 79, no. 2, pp. 229–238.

Newcombe, C. L.
1929. The crayfishes of West Virginia. Ohio Journ. Sci., vol. 29, pp. 267–288.

Ortmann, A. E.
1902. The geographical distribution of freshwater Decapods and its bearing upon ancient geography. Amer. Philos. Soc., vol. 41, no. 171, pp. 217–400, figs. 1–8.
1905. The mutual affinities of the species of the genus *Cambarus*, and their dispersal over the United States. Proc. Amer. Philos. Soc., vol. 44, no. 180, pp. 91–136, 1 map.
1913. The Alleghenian Divide and its influence upon the freshwater fauna. Proc. Amer. Philos. Soc., vol. 52, no. 210, pp. 287–390, 3 pls.
1931. Crawfishes of the Southern Appalachians and the Cumberland Plateau. Ann. Carnegie Mus., vol. 20, no. 2, pp. 61–160.

Parish, C.
1948. A contribution toward a knowledge of the crayfish *Cambarus longulus dasydactylus*, with special reference to the annulus ventralis. Unpublished master's thesis, University of Virginia.

Reid, G. K.
1961. Ecology of inland waters and estuaries. xvi+375 pp.

Snodgrass, R. E.
1952. A textbook of arthropod anatomy, viii+363 pp.

U.S. GOVERNMENT PRINTING OFFICE:1966